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Paragus caligneus sp. nov., a new Afrotropical species of flower fly (Diptera: Syrphidae)

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Abstract. A new species of flower fly (Diptera: Syrphidae) is described, *Paragus caligneus* sp. nov. A full description with images is given, as well as a species key for the subgenus *Afroparagus* Vujić & Radenković, 2008 and a modification of the identification key for *Paragus* subgenera. Molecular sequences from mitochondrial cytochrome c oxidase I (COI) and nuclear ribosomal 28S rRNA genes were analyzed to evaluate the monophyly of *Afroparagus*. All four *Paragus* subgenera were recovered as monophyletic, although support values for *Afroparagus* were very low.

Key words. Diptera, Syrphidae, flower flies, *Afroparagus*, new species, COI, 28S, Central African Republic, Afrotropical Region

Introduction

Paragus Latreille, 1804 (Diptera: Syrphidae) is the single genus of the tribe Paragini, with almost 100 described species worldwide (Vujić et al. 2008, Thompson 2013). The tribe, member of the subfamily Syrphinae, is defined by morphological characters of the male genitalia (Glumac 1960, Dušek & Láska 1967, Vockeroth 1969), but adults are easy to identify due to singular morphological characters, such as tergum 1 well developed, partial fusion of terga, or terga being punctate. The adults feed on pollen and nectar from flowers, as it is usual for syrphines, but larvae of *Paragus* feed mostly on soft-bodied Hemiptera and some other insects (see review in Rojo et al. 2003).

The phylogenetic relationships between *Paragus* and other tribes and genera remain uncertain (Dušek & Láska 1967, Vockeroth 1969), although molecular evidences indicate a close relationship with Neotropical and Oriental/Afrotropical genera (Mengual et al. 2008, 2012). Vujić et al. (2008) revised the genus using both morphological and molecular data and proposed a subdivision in four subgenera, including the classical subgenera *Paragus* s. str. and *Pandasyopthalmus* Stuckenberg, 1954, and describing two new subgenera, *Afroparagus*

Vujić & Radenković, 2008 and *Serratoparagus* Vujić & Radenković, 2008. In addition, they recognize two species groups within the subgenus *Pandasyopthalmus*, the *tibialis*-group and the *jozanus*-group.

The current knowledge of the genus *Paragus* in the Afrotropical Region is based mainly on the revisions of Stuckenberg (1954a,b) and a number of subsequent species descriptions by Kassebeer (1998, 1999a,b, 2000, 2001), Whittington (1998) and Smit & Gutiérrez-Chacón (2008). Previously, Curran (1938) presented a key to the Afrotropical species, although quite incomplete. All four subgenera are present in the Afrotropical Region with a total of 28 species distributed as follows according to De Meyer (1998) and Vujić et al. (2008): 1 *Afroparagus* (plus the new species described here), 21 *Pandasyopthalmus*, 1 *Paragus*, and 4 *Serratoparagus*. While the subgenus *Pandasyopthalmus* has its largest radiation in the Afrotropical Region, a single species of *Afroparagus* is known worldwide, *Paragus* (*Afroparagus*) *borbonicus* Macquart, 1842. This *Afroparagus* species is abundant and widespread throughout most of Africa (see Dirickx 1994: map 51) and is regularly present in wet grassland and rice fields.

Here we describe a new species of the subgenus *Afroparagus*, *Paragus caligneus* sp. nov., the second known species after *P. borbonicus*. We provide a full description with images, a species identification key for *Afroparagus* and a modification of the subgenera identification key by Vunć et al. (2008) to accommodate the new species. In addition, we reanalyze the molecular data of Vunć et al. (2008) including the new *Afroparagus* species to study the support of the subgenus.

Material and methods

Terminology follows Thompson (1999), Vujić et al. (2008) and Mengual (2012). The term granulation (Torre-Bueno 1937) refers to the ornamentation or pattern of markings of the abdominal terga, i.e. elevations on the body surface named granulum (granula in plural) (Brown 1956). Identification and location labels are indicated with quotation marks (""), and each line on the label is separated by a double forward slash (//). Handwritten information on labels is indicated in italics.

The EVENHUIS (2009) standard acronyms were used for the following entomological collections:

ASWG Axel Ssymank, Wachtberg, Germany;

CZUP Czech University of Life Sciences, Prague, Czech Republic;

ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

In the material examined, the collections where the specimens are deposited are indicated between square brackets after each specimen.

Illustrations of male and female abdomens were composed using Auto-Montage Pro 5.03 and CombineZP software based on images of pinned specimens taken with a QImaging Micro-Publisher 5.0 RTV camera mounted on a Leica Z6 APO. All measurements are in millimetres and were taken using a graticule in a Leica M165C and a Zeiss SV11 microscope. Drawings were made with a Zeiss drawing mirror attached to the SV11. Body length was measured

from the anterior oral margin to the posterior margin of the abdomen in lateral view. Wing length was measured from the wing tip to the basicosta.

Phylogenetic analyses. We used the molecular data from Vujić et al. (2008) to study the phylogenetic placement of the new species, *Paragus caligneus*. We used the sequences of a large fragment of mitochondrial cytochrome c oxidase subunit I (COI) and the region D2–D3 of the nuclear 28S rRNA gene (see Table 1). We followed the laboratory protocols of Mengual et al. (2008a,b; 2012) to extract, amplify and sequence both gene fragments. In addition, we

Table 1. Taxon sampling used in the molecular analysis, including GenBank accession numbers.

Taxon	COI	28S	Source
Paragus albifrons (Fallén, 1817)	AY476846	_	GenBank
Paragus ascoensis Goeldlin & Lucas, 1981	AY476840	_	Vuлć et al. (2008)
Paragus atratus de Meijere, 1906	AY476842	AY476875	Vuлć et al. (2008)
Paragus azureus Hull, 1949	not submitted	_	G. Ståhls (unpubl. data)
Paragus bicolor (Fabricius, 1794)	AY476857	AY476873	Vuлć et al. (2008)
Paragus borbonicus Macquart, 1842	AY476850	AY476882	Vuлć et al. (2008)
Paragus caligneus sp. nov.	KJ158454	KJ158455	this study
Paragus capricorni Stuckenberg, 1954	not submitted	_	G. Ståhls (unpubl. data)
Paragus coadunatus (Rondani, 1847)	AY174467	AY476865	Vuлć et al. (2008)
Paragus crenulatus I Thomson, 1869	AY476862	AY476880	Vuлć et al. (2008)
Paragus crenulatus II Thomson, 1869	AY476863	AY476879	Vuлć et al. (2008)
Paragus finitimus Goeldlin, 1971	AY476851	AY476878	Vuлć et al. (2008)
Paragus haemorrhous Meigen, 1822	AY174470	AY476866	Vuлć et al. (2008)
Paragus hyalopteri Marcos-García & Rojo, 1994	AY476845	_	Vuлć et al. (2008)
Paragus longiventris Loew, 1858	AY476859	AY476887	Vuлć et al. (2008)
Paragus manensis Kassebeer, 1999	AY476860	AY476883	Vuлć et al. (2008)
Paragus nr. goeldlini Thompson, 1992	AY174463	_	Vuлć et al. (2008)
Paragus nr. minutus Hull, 1938	AY275522	_	GenBank
Paragus nr. politus Wiedermann, 1830	AY174461	AY476884	Vujić et al. (2008) and GenBank
Paragus pecchiolii Rondani, 1857	AY476844	AY476864	Vuлć et al. (2008)
Paragus punctulatus Zetterstedt, 1838	AY476847	AY476877	Vuлć et al. (2008)
Paragus pusillus Stuckenberg, 1954	AY476861	AY476881	Vuлć et al. (2008)
Paragus quadrifasciatus Meigen, 1822	AY174464	AY476874	Vuлć et al. (2008)
Paragus sexarcuatus Bigot, 1862	AY476852	_	Vuлć et al. (2008)
Paragus strigatus Meigen, 1822	AY476843	AY476876	Vuлć et al. (2008)
Paragus testaceus Meigen, 1822	AY476848	AY476870	GenBank
Paragus tibialis (Fallén, 1817)	AY174468	AY476867	Vuлć et al. (2008)
Paragus villipennis Thompson, 1992	AY476858	AY476886	Vuлć et al. (2008)
Pipiza quadrimaculata (Panzer, 1804)	EU431506	EU431474	GenBank
Pipizella viduata (Linnaeus, 1758)	AY261695	AY261742	Vuлć et al. (2008)
Trichopsomyia flavitarsis (Meigen, 1822)	AY212798	AY261729	Vuлć et al. (2008)

included COI sequences of *Paragus albifrons* (AY476846) and *P. nr. minutus* (AY275522), and COI and 28S sequences of *P. testaceus* (AY476848 and AY476870 respectively). These sequences were downloaded from GenBank.

The protein-coding COI gene was aligned manually and no gaps were necessary in this alignment. The final COI data matrix contained a total of 1,128 nucleotide characters. The region D2–D3 of the 28S rRNA gene was aligned using the secondary structure of this gene following Mengual et al. (2012). Small regions of ambiguous alignment were included in the phylogeny inference analysis. The combined analysis of these two genes comprised a total of 1,747 bp of DNA for 32 taxa, including gaps.

DNA sequence data were analyzed using maximum likelihood and Bayesian inference analyses. For both analyses the dataset was divided in four partitions: 28S gene, first codon position of COI, second codon position of COI, and third codon position of COI. The best model for each partition was determined using jModelTest 0.1.1 (POSADA 2008, 2009) under the Akaike Information Criterion (AIC), as recommended by POSADA & BUCKLEY (2004). The model chosen for 28S was GTR + G, TIM2 + G for COI position 1, TPM1uf + G for COI position 2, and HKY + G for position 3 of COI gene. Analytical runs were performed on the Topaz cluster at the National Museum of Natural History, Smithsonian Institution, Washington DC.

We analyzed the data under the recommended models using Garli-Part v0.97 (ZWICKL 2006, 2010) and treated gaps as missing data. Bootstrap support values (BP) were estimated from 1,000 replicates using the same independent models in Garli-Part v0.97. MrBayes 3.2 (HUELSENBECK & RONQUIST 2001, RONQUIST & HUELSENBECK 2003) was used for Bayesian inference. We ran our analysis specifying a separate GTR + G model for each partition, where each partition has its own set of parameters. Six runs, with four chains each were performed simultaneously for 15,000,000 generations which were sufficient to bring the convergence (average standard deviation) to a value < 0.005 (Ronquist et al. 2005), sampling trees every 2,500 generations. The initial 1,500 trees (25 %) were discarded as burn-in and clade support was calculated using Bayesian posterior probabilities (PP).

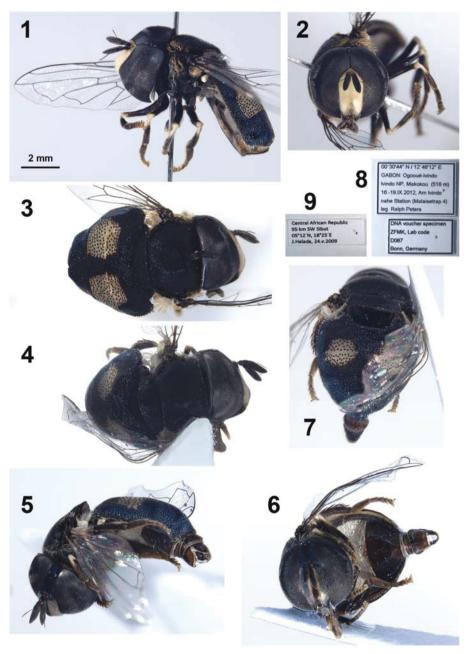
Taxonomy

Paragus caligneus sp. nov.

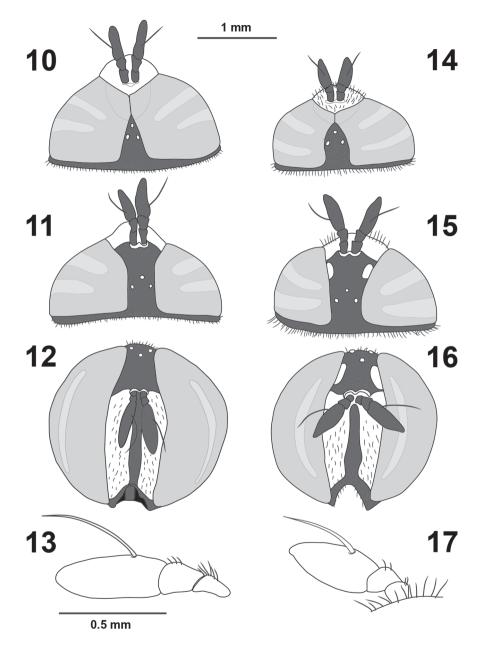
(Figs 1-13, 18-21)

Type locality. Gabon, Ogooué-Ivindo, Ivindo National Park, Makokou, 518 m a.s.l., 00°30′44″N, 12°46′12″E. Type material. Holotype: ③, "00°30′44"N // 12°46′12"E // GABON: Ogooué-Ivindo // Ivindo NP, Makokou (518 m) // 16-19.IX.2012, Am Ivindo // nahe Station (Malaisetrap 4) // leg. Ralph Peters" "HOLOTYPE // Paragus caligneus Ssymank & Mengual [red label]" [ZFMK]. Paratype: ♀, "Central African Republic // 95 km SW Sibut // 05°12'N, 18°25'E // J. Halada // 24.V.2009", "PARATYPE // Paragus caligneus Ssymank & Mengual [yellow label] [CZUP].

Description. *Male. Head* (Figs 1–3, 6, 10–13). Eye with two vertical vittae of white pile among short dark pile. Eye contiguity ca. 1/3 of length of vertical triangle. A patch of enlarged ommatidia in front of vertical triangle on both sides of eye contiguity. Angle of eye approximation ca. 90°. Vertical triangle polished black with a small whitish pollinosity anterior to anterior ocellus, otherwise short black pilose. Occiput with whitish pile on ventral 1/2, darker above with only black pile on dorsal 1/3. Face yellow with short yellow pile (max. ca. 1/2 length



Figs 1–9. *Paragus caligneus* sp. nov. 1–3 – holotype male; 1 – lateral view; 2 – frontal view; 3 – dorsal view. 4–7 – paratype female; 4 – dorsal view; 5 – lateral view; 6 – frontal view; 7 – posterior view. 8 – holotype male, labels. 9 – paratype female, label.



Figs 10–17. 10–13 – *Paragus caligneus* sp. nov.; 10 – male head, dorsal view; 11 – female head, dorsal view; 12 – female head, frontal view; 13 – male antenna, lateral view. 14–17 – *Paragus borbonicus* Macquart, 1842; 14 – male head, dorsal view; 15 – female head, dorsal view; 16 – female head, frontal view; 17 – male antenna, lateral view.

of scape), without medial black vitta, but weak facial knob translucent yellow and therefore darker than sides of face. Peristome and gena black, clypeus subquadrate and brownish black. Antennae long, basoflagellomere ca. 2.5 times as long as wide, ventrally in the basal corner slightly brownish-red; arista brown, inserted at 1/3 of length of basoflagellomere, slightly surpassing tip of basoflagellomere (Fig. 13); total length of arista slightly shorter than length of basoflagellomere; lunula yellow. Proboscis with large whitish labellum.

Thorax (Figs 1, 3, 4, 5). Scutum polished black, no pollinose maculae present, coarsely granulate with very short black pile. Long yellow to orange pile laterally before the suture and stiff yellow slightly thickened pile on postalar callus. Pleuron black, long yellow pile on an an episternum, long white pile on dorsal part of katepisternum. Scutellum also polished black and coarsely granulate with short black pile, ca 1/10 of the scutellum-length. Scutellum subrectangular, ca. 3 times as wide as long, hind margin also granulate as dorsal surface.

Wing. Hyaline and almost completely bare of microtrichia, at most with a few scattered microtrichia. Alula oval, ca. 2.5 times longer than wide, with sparse microtrichia along border, central and basal part bare. Spurious vein not reaching distal cross vein. Pterostigma whitish.

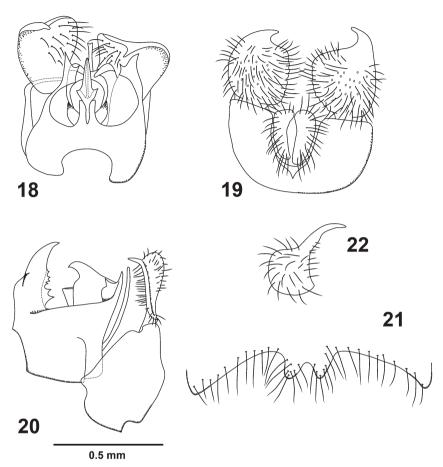
Legs. Femora black with narrow sharply delimited yellow apex (knee). Pile on the back-side and ventrally mostly yellow. Front and middle tibia apically ca. 2/3 black, proximal 1/3 yellow. Metatibia apically 3/4 black, thickened and laterally compressed, dorsally with dense long black pile, ventrally short black pile, apical ventral part with yellow-reddish pile. Basal three tarsomeres brownish-black dorsally, apical two tarsomeres dark yellow.

Abdomen (Figs 3, 4, 7). First five terga fused laterally; terga 3–5 bluish black polished with very coarse granulation (granula). Terga 2 and 3 with two subquadrate large ivory maculae (greenish in fresh material), well separated from each other and from the side margin. Granulation in the ivory maculae with black dots. Tergum 4 completely bluish black with narrow almost indiscernible lateral depression. Granula on the surface of terga and on lateral margin with short apical black pile. Sternum 1 brownish, sterna 2–3 white, sternum 4 brown with distal margin bearing a bifurcate medial extension with long pile (Fig. 21). Sterna with long white pile.

Male genitalia (Figs 18–20). Epandrium in the narrower middle part is only half as long as cercus in dorsal view; surstylus large, almost as high as epandrium, straight with a short apical tooth or hook bent inwards.

Female (Figs 4–7, 11, 12). Similar to male except for normal sexual dimorphism and: Face yellow with a narrow medial black vitta about 1/5 width of face, reaching up to the base of the antennae (Fig. 12). Frons ca. 1/6 to 1/7 head width at level of posterior ocelli, polished black without pollinose maculae, subparallel margins in upper half of frons (Fig. 11) and then broadening towards antennal sockets in lower half. Whitish maculae on abdomen smaller than in male and more rounded (Fig. 7). Metatibia of normal shape (not compressed or enlarged as in the male), but with the same fringe of long dark pile dorsally. Occiput with white pile reaching further up than in male, but in dorsal part with some black flattened pile among the whitish ones. Arista slightly shorter than in male, not surpassing the tip of the basoflagellomere.

Length. Body: 5.8 mm (holotype), 6.7 mm (paratype); wing 4.9 mm (holotype), 5.0 mm (paratype).



Figs 18–22. 18–20 – *Paragus caligneus* sp. nov., male genitalia. 18 – ventral view; 19 – dorsal view; 20 – lateral view. Fig. 21. *Paragus caligneus* sp. nov., posterior margin of sternum 4. 22 – *Paragus borbonicus* Macquart, 1842, surstylus in dorsal view.

Differential diagnosis. Paragus caligneus sp. nov. can be clearly recognized from all other known Afrotropical species by the large, whitish to green abdominal maculae with black dots. It can be easily distinguished from *P. borbonicus*, the only other known species of Afroparagus, by a series of morphological characters summarized in the diagnostic Table 2. The most evident differences are: the coloration of tergum 3, the coloration of the legs (femora largely black with narrow yellow apex in *P. caligneus*, while *P. borbonicus* has femora with much broader yellow apical parts; protibia 2/3 brown apically, while *P. borbonicus* has completely yellow protibia); the dense, long brown-black pile dorsally on the metatibia (white pile in *P. borbonicus*); and very short pile in general on scutum, scutellum and face in comparison with *P. borbonicus*. The holotype male of *Paragus caligneus* has a bifurcate extension in the middle of the posterior margin of sternum 4, and male genitalia of both species are completely

different (see Stuckenberg 1954a: Figs 41–43). The female of *P. caligneus* does not have pollinose maculae on the frons, while *P. borbonicus* females have white pollinose maculae at the eye margin. Females of both species have a medial black facial vitta connected to a usually black oral margin. Males of *P. borbonicus* have the face completely yellow, but the holotype male of the new species has yellow face and black gena.

Etymology. The specific epithet is derived from the Latin *caligo*, meaning dark, gloomy (Brown 1956: 148). Species epithet to be treated as an adjective.

Biology. Larvae unknown, presumably zoophagous, probably on aphids as most other larvae of known species of the genus *Paragus*. Holotype collected in a Malaise trap alongside the Ivindo river; no other information available.

Distribution. Known only from Gabon (holotype \lozenge) and Central African Republic (paratype \lozenge).

Key to subgenera of Paragus

(modified and simplified from Vuлс et al. 2008)

Eye with vertical alternate vittae (bands) of pile reflecting light differently.
 Eye uniformly pilose.
 Pandasyopthalmus Stuckenberg, 1954
 Scutellum with conspicuous teeth (minimum about double length of diameter) on posterior margin; in dorsolateral view eyes with two dark and three more distinct, white, dorso-ventral vittae of pile.
 Serratoparagus Vujić & Radenković, 2008
 Scutellum without conspicuous teeth on posterior margin (either smooth or granulate with granula of about same length or height as diameter); in dorsolateral view eyes with two white dorso-ventral vittae of pile among dark pile.
 Tergites 1–5 completely fused, at least laterally. Male genitalia: epandrium in narrower part 1/2 to 2/3 the length of the cercus (Fig. 19). Afrotropical species.
 Afroparagus Vujić & Radenković, 2008
 Only tergites 1–2 completely fused. Male genitalia: epandrium in narrower part twice as long as cercus. Mainly Holarctic species.

Identification key for Afroparagus species

- Tergum 3 black with two rounded whitish-yellow to green maculae, well separated from each other and from lateral margins; granulation black on the maculae. Femora brownish-black except narrow yellow apex (Fig. 1); metatibia with long, dense brown to black pile dorsally; protibia brown in distal 2/3; protarsi darkened. Posterior margin

Table 2. Differential morphological characters to distinguish the species of Afroparagus.

Character	Paragus caligneus sp. nov.	Paragus borbonicus
Frons, 🖁	Polished black, no trace of pollinose maculae.	Lower frons with narrow pollinose maculae along eyes
Face and frons, ♀	Narrower (see Figs. 11, 12), dorsal margins subparallel.	Wider (see Figs 15, 16), frons widening gradually towards antennae.
Vertical triangle, ♂	Vertical triangle narrow, with straight sides (see Fig. 10).	Vertical triangle broad, with sides bulged (see Fig. 14).
Eye contiguity, \circlearrowleft	Eye contiguity longer than height of ocellar triangle.	Eye contiguity short, shorter than height of ocellar triangle.
White pile on lower face	Short, shorter than half the length of scape in side view.	Very long, almost as long as scape in side view.
Occiput	Dorsal part with at least some black flattened pile among the whitish ones.	Dorsal part with only yellow flattened pile.
Terga 3-5	Bluish polished, very coarse granulation.	Black polished, fine granulation.
Tergum 3	With two rounded whitish-yellow to green maculae, well separated from each other and from lateral margins. Granulation with black dots on the maculae.	Broad yellow fascia, reaching close to the mostly black side margin, in antero- lateral corner, often narrowly reaching lateral margin. Granulation completely yellow also on yellow fascia.
Tergum 4	Completely bluish-black polished, no depression present.	Narrow yellow elongated macula close to the anterior margin in a transverse groove.
Sternum 4, posterior margin, \circlearrowleft	With a bifurcate medial projection on the posterior margin (Fig. 21).	Smoothly curved, no projection at posterior margin.
Surstylus	Short hook or tooth at the end, maximum 2 times as long as wide (Fig. 19).	Long hook at the end, ca. 4–5 times as long as wide (Fig. 22).
Proboscis	Labellum whitish, larger and broadly oval.	Labellum small, brownish-black with narrowed oval tip.
Metatibia	With long dense brown to black pile dorsally.	With long white pile dorsally.
Protibia and tarsi	Protibia brown on apical 2/3, protarsi darkened.	Completely yellow.
Femora 1–3	All femora brownish-black, except very narrow yellow apex.	F1 basal 1/4, F2 basal 1/2 and F3 basal 2/3 sharply delimited black, apical parts yellow.
Scutellar pile	Very short pile.	Long pile, on disc ca. 1/3 of scutellum length, on posterior margin ca. 1/2 scutellum length
Scutellum margin	Smooth.	Granulate, laterally extended into short teeth on the posterior margin.

Phylogenetic results

Bayesian inference and Maximum Likelihood (ML) reported two similar topologies, in which the relationships among the four *Paragus* subgenera are not well resolved; with deep nodes with very low values (less than 0.5 or 50 % respectively). The likelihood score for the best ML tree (Fig. 23) was -8463.463783. The topology of the most likely tree compares favorably with the majority rule consensus tree resulting from Bayesian inference (Fig. 24).

Species belonging to the same subgenus are resolved together with moderate to high bootstrap values and Bayesian posterior probabilities (BPP). Subgenera *Pandasyopthalmus*, *Paragus* and *Serratoparagus* seem to be well supported (bootstrap values 79, 80, 100 and BPP 1, 1, 1 respectively). On the other hand, *Afroparagus* is resolved with very low support value.

Paragus s.str. species were clustered together with 80% bootstrap value and a high BPP of 1. In both analyses, the internal relationships among *Paragus* s.str. species were not well resolved, with the exception of the sister group relationship between *P. bicolor* (Fabricius, 1794) and *P. testaceus* Meigen, 1822, and between *P. quadrifasciatus* Meigen, 1822 and *P. hyalopteri* Marcos-García & Rojo, 1994. On the contrary, *Pandasyopthalmus* and *Serratoparagus* species are all dichotomous, resolved in a similar way as reported by Vujić et al. (2008). The two species of *Afroparagus*, *P. borbonicus* and *P. caligneus* sp. nov., were resolved as sister groups with a very low support (bootstrap value less than 50% and BPP = 0.62).

Discussion

The new species belongs to the subgenus *Afroparagus* according to the characters given by Vujić et al. (2008), with two vittae of white pile in the eyes, epandrium in narrower part 1/2 the length of the cercus, and terga 1–5 fused. However, the posterior margin of the scutellum has a series of coarse granula sligthly extended into very short "teeth-like" protuberances, similar as the ones in the subgenus *Serratoparagus*. These granula are about as long as wide in *P. caligneus* sp. nov. and can be found on the whole surface of the scutellum and scutum. On the other hand, *Serratoparagus* has teeth at the posterior margin of the scutellum which are usually 2–3 times as long as wide. *Paragus* (*Afroparagus*) borbonicus has an oval scutellum with long pile, much thinner granulation and no granula at the posterior margin.

Male genitalia of *P. caligneus* partly fit the diagnostic characters of *Afroparagus* given by Vunć et al. (2008). However, there are marked differences such as the presence of a large lingual, the shape of the surstylus, and the emargination on posterior margin of the sternum 4.

We want to point out the very low support values obtained in the phylogenetic analyses and the molecular differences between *P. borbonicus* and *P. caligneus* sp. nov. (see branch lengths in Figs 23, 24). This very low support might indicate that they are the closest species included in our analyses, although they might not belong to the same species group.

The need to modify the subgeneric key to accommodate our new species, plus the big differences in male genitalia and the very low support of *Afroparagus* in the molecular analyses suggest that *P. caligneus* sp. nov. might belong to a separate evolutionary lineage, old enough to accumulate large molecular difference.

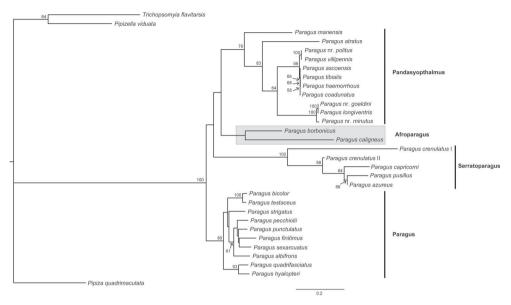


Fig. 23. Phylogram of the best tree from a maximum likelihood search of the combined dataset using Garli-part v0.97 ($\ln L = -8463.463783$). Numbers above nodes are maximum likelihood bootstrap support values (>50%).

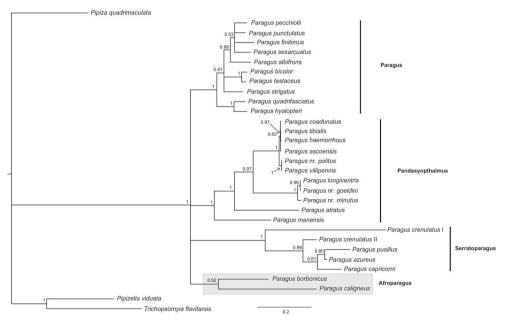


Fig. 24. Majority-rule consensus tree from the Bayesian analysis using MrBayes. The Bayesian posterior probability values (>0.5) are given above the nodes.

Acknowledgements

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